# ANT-MEDIATED SEED DISPERSAL OF THE RARE CHAPARRAL SHRUB *FREMONTODENDRON DECUMBENS* (STERCULIACEAE)

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ABSTRACT

Ant-mediated seed dispersal is unusual for California chaparral shrubs. This study documents dispersal of the elaiosome-bearing seeds of *Fremontodendron decumbens* by the harvester ant *Messor* (=*Veromessor*) *andrei*. Seeds were released from capsules over a period of ca. 2 mo during the summer, but the timing of release varied between years. Ants were strongly attracted to the elaiosome portion of diaspores rather than the seed portion, and carried elaiosome-bearing seeds up to 12 m from *F. decumbens* shrubs. Because ant nests never occurred under shrub canopies, seeds were transported from beneath parent shrubs to nests located in gaps in the existing shrub cover. Some seeds (at least 5%) that were taken into ant nests were apparently consumed by ants, 45% were ejected intact and left on nest middens within 65 cm of nest entrances, and the remainder were not found and may have remained within the nests. The seed coat of *F. decumbens* was greatly (3-fold) thickened near the elaiosome, suggesting an adaptation to discourage ants from consuming seeds. Elaiosomes contained little moisture but significant amounts of fat, protein, and carbohydrates. Each elaiosome contained 8.8% of the total energy content of a diaspore. In energetic terms, the cost to *F. decumbens* of building elaiosomes was relatively small (an 8% reduction in seed output). Elaiosomes also were consumed by small invertebrates and decomposers, so that elaiosomes were absent from diaspores after 2 mo in the litter layer.

Chaparral is a shrub-dominated vegetation type that has long been of interest for many reasons, including its association with both a Mediterranean-type climate and periodic fires (Keeley 1989). Numerous studies of many aspects of chaparral biology have been undertaken (Keeley 1989), but detailed studies of seed dispersal mechanisms of chaparral species (particularly shrub species) are few (Hanes 1977). In some cases (e.g., Bullock 1978; Keeley 1991), dispersal mechanisms are inferred based upon morphologic characteristics of fruits or seeds.

Ant-mediated seed dispersal (myrmecochory) is relatively common in arid areas of Australia (Berg 1975; Buckley 1982) and South Africa (Milewski and Bond 1982) but seems comparatively rare in California chaparral. Conclusive documentation of the importance of myrmecochory has been demonstrated for only one chaparral shrub, *Dendromecon rigida* Benth. (Berg 1966; Bullock 1974, 1989). Myrmecochory is likely if fruits or seeds bear elaiosomes,

food bodies that attract ants and induce them to transport diaspores to their nest (Beattie 1985). Although a comprehensive study has not been conducted, few chaparral shrub species possess elaiosomes. A study by Keeley (1987) of 45 shrub species identified *Fremontodendron* (in particular *F. californicum* (Torrey) Cov., Sterculiaceae) as the only chaparral shrub other than *Dendromecon* that possesses elaiosome-bearing seeds. Keeley (1991) predicted that seeds of *Fremontodendron* were ant-dispersed.

Boyd and Serafini (1992) studied the reproductive biology of *Fremontodendron decumbens* Lloyd, a rare chaparral species with elaiosome-bearing seeds found in the foothills of the Sierra Nevada (Kelman 1991). Observations during that research indicated that ants transported seeds of *F. decumbens*. Keys and descriptions in Smith (1947) and Wheeler and Wheeler (1973) identified the ants as harvester ants of the species *Veromessor andrei* Mayr (Hymenoptera: Formicidae). The genus *Veromessor* is now included in *Messor,* so that the currently accepted name is *Messor andrei* (Mayr) (see discussion in Bolton 1982). This study documents and describes this apparent chaparral ant-plant relationship with *F. decumbens*.

## METHODS

*Study species. Fremontodendron decumbens* grows only within a few km of the summit of Pine Hill in El Dorado County, California. Most plants are found within the Pine Hill Ecological Reserve, which encompasses the majority of the hill. *Fremontodendron decumbens* grows mainly on relatively rocky ridgetops, along with typical chaparral dominants such as *Arctostaphylos glauca* Lindl., *Adenostoma fasciculatum* H. & A., and *Heteromeles arbutifolia* M. Roem.

The ecologic life cycle of *F. decumbens* has been characterized by Boyd and Serafini (1992) and Boyd (1994), and will be summarized briefly here. Plants initiate flower buds in late winter. By the time flowers open in April, most of the flower buds (80%) have been destroyed by insect larvae. Flowers are efficiently pollinated by native solitary bees (Boyd 1994), but developing fruits are attacked by insect larvae and 70% are destroyed prior to maturity. Surviving fruits dehisce during summer and release seeds into the litter under shrubs. Seeds possess an orange-yellow elaiosome (technically a caruncle, Kelman 1991) on the distal end of the seed. Seeds are eaten by rodents and 90% of seeds placed into the litter under *F. decumbens* shrubs are destroyed during a one-year period (Boyd and Serafini 1992).

*Messor andrei* (Mayr) is found throughout the length of California (Creighton 1950). It is a group-foraging species, forming a column of workers many meters in length that explores and harvests mate-

rials from an area near the nest during a foraging period (Cook 1953). These ants typically form a midden near the nest opening in which they deposit excavated soil and discarded plant material. Harvester ants generally act as seed predators (Reichman 1979) and have been reported to decrease the effectiveness of post-fire grass seeding in California chaparral (Howard 1950), although they have been recorded to disperse elaiosome-bearing seeds (O'Dowd and Hay 1980). When handling an elaiosome-bearing seed, the elaiosome is removed and the seed is ejected onto the midden (Creighton 1950).

*Study sites.* Study sites were located on the main east–west ridge of Pine Hill. The ridges of Pine Hill were disturbed in 1969 by the cutting of firebreaks. Unfortunately, these ridges also contained the largest stands of *F. decumbens.* Most of the shrub species present, including *F. decumbens,* were not killed but re-sprouted from the cut stumps. They recovered to form a stand that was 13 yr old in 1982, when the studies described here began (Boyd 1994).

Both of the sites used in this study were located on the east-west ridge located east of the summit of Pine Hill. Site 1 contains the largest stand of *F. decumbens* currently known. Even so, the dominant chaparral shrub on this site was *Adenostoma fasciculatum.* Site 2 was ca. 150 m from the summit and ca. 200 m west from Site 1, in a rocky area containing a few *Pinus ponderosa* Dougl. ex P. & C. Lawson and *P. sabiniana* Dougl. Most of the shrub cover on this site was *Adenostoma fasciculatum* and *Arctostaphylos glauca. Fremontodendron decumbens* shrubs were scattered among shrubs of other species on both sites. Total cover of *F. decumbens* was less than 5% in both locations.

*Ant activity and seed availability.* Observations of ant activity patterns were made at irregular intervals during five years (1982–1986). Most of the observations were made on Site 1. I determined when seeds became available to foraging ants by monitoring the timing of fruit dehiscence on 53 branches located on 17 shrubs on Site 1. Branches were censused at approximately biweekly intervals during the late spring and summer during five years (1982–1986) to count numbers of dehiscing fruits. Precipitation records for these years were obtained from the weather station in Placerville, El Dorado County (NOAA 1982–1986). This station was the closest both geographically (16 km E of Pine Hill) and elevationally (576 m versus 627 m for Pine Hill) to the study sites.

*Harvester ants as seed dispersers.* I compared the attractiveness of seeds to harvester ants by a choice test, using seeds in three conditions: fresh seeds collected from Pine Hill shrubs with the elaiosomes removed, similar seeds with the elaiosomes attached, and

old seeds taken from the seed bank beneath *F. decumbens* shrubs growing in the Arboretum at the University of California, Davis. Seeds from the Arboretum seed bank were collected by hand-sifting the litter underneath the shrubs. These old seeds were weathered and their elaiosomes had disappeared (presumably by the action of decomposers, as no harvester ants were present in the Arboretum). By using seeds in these three conditions, the importance to ant attractiveness of two factors could be tested: presence of the elaiosome and freshness of the seeds. Seeds were marked with nail polish and allowed to air dry for 2 weeks before use. Subsequent handling was done with a metal spoon to minimize application of human scent to the seeds. Caches containing five seeds of each type were placed in the path of foraging columns of *M. andrei* in September 1983. A total of 20 caches were placed, using ants foraging from four nests. I counted numbers of seeds remaining in each cache at hourly intervals for 3 hours. Numbers of seeds of each type remaining were compared by the Kruskal-Wallis test, and means separation was accomplished by Tukey-type multiple comparisons as described by Zar (1984).

Active *M. andrei* middens on Sites 1 and 2 were canvassed for the presence of seeds at the end of the period of capsule dehiscence of *F. decumbens.* Most middens examined were checked in 1983, but some were checked in 1984. Any *F. decumbens* seeds present were counted and the distance from each midden to the edge of the nearest *F. decumbens* canopy was measured. All ant middens on both study sites were characterized by measuring the distance from the nest entrance to the edge of the canopy of the nearest individual of any shrub species and to the edge of the nearest *F. decumbens* canopy.

*Fates of seeds taken by ants.* I supplied seeds to ant nests in order to determine the fates of seeds taken into nests. Fresh seeds were marked with nail polish as above and placed in small caches in the path of foraging ant columns. Seed removal was recorded and middens of each nest were checked for discarded seeds at irregular intervals for 1–2 weeks. Discarded marked seeds (and any discarded unmarked seeds) were counted and the distance of each intact seed from the nest entrance was measured.

In early October 1983, I followed the short-term removal of *F. decumbens* seeds from ant middens on Site 1. Five marked seeds, previously recovered from middens (so that they lacked elaiosomes) were placed on each of five middens. Locations of seeds were marked with toothpicks placed within 1 cm of the seed. I counted the remaining seeds after 10, 30, 57, and 120 days.

The above studies revealed that some of the seeds taken into nests were destroyed because empty seed coats were recovered from the

middens. I hypothesized that seed coat thickness may be greater under the elaiosome to protect the seed from ants during removal of the elaiosome. To test this hypothesis, I longitudinally sectioned 45 seeds and measured seed coat thickness with the ocular micrometer of a dissecting microscope at 65× magnification. I measured thickness at three places: in the middle of the zone of elaiosome attachment, at the end of the seed opposite the elaiosome, and at a point on the side halfway between the first two. Data were analyzed by one-way ANOVA with pairwise comparisons using Fisher's PLSD test.

*Elaiosome longevity.* I determined elaiosome longevity in the litter layer under shrubs by stapling 10 fresh diaspores possessing relatively large elaiosomes into each of 45 sleeves made of 1.4-mm mesh fiberglass screen. Nine sleeves were placed under shrubs at each of five locations on Site 1 in mid-September 1983. I scraped the litter off the soil, placed the sleeves on the soil surface, covered them with a screen of 7-mm mesh hardware cloth to prevent disturbance by rodents, and replaced the litter. After weighing the elaiosomes of a sample of diaspores at the start of the experiment, I removed a sleeve from each location at irregular intervals over a 7-month period, allowed them to air-dry if the litter was wet, and removed and weighed the elaiosomes.

*Nutritional analysis.* Nutritional analysis of seeds and elaiosomes was performed to determine the investment of *F. decumbens* in each diaspore component, as well as the value of each to the diet of the ants. Elaiosomes and seeds from a mass collection of diaspores collected from Pine Hill shrubs were weighed individually, composited, and analyzed for nutritional quality. Subsamples of both elaiosomes and seeds were used to quantify protein, ash, fat, fiber, and soluble carbohydrate composition. Samples of about 2 g were used to determine elaiosome and seed nitrogen contents by Kjeldahl analysis and protein contents were calculated as %N multiplied by 6.25 (Jones 1984). Ash contents were determined by ignition of a 5 g sample at 600°C for 2 hr. Fat content was measured by ether extraction of a 2 g sample followed by evaporation of the ether and weighing of the residue (Jones 1984). Crude fiber was determined as the percent of material in a 2 g sample that was insoluble in dilute acid and base (Horwitz 1965). Soluble carbohydrate was determined by subtracting the sum of protein, ash, fat and fiber from 100%. Dietary energy contents of elaiosomes and seeds were calculated from protein, fat, and carbohydrate contents by the method of Davidson and Morton (1984).

Total energy in seeds and elaiosomes was determined by bomb calorimetry, using a Gallenkamp Autobomb (automatic adiabatic bomb calorimeter). I separated a mass collection of diaspores from
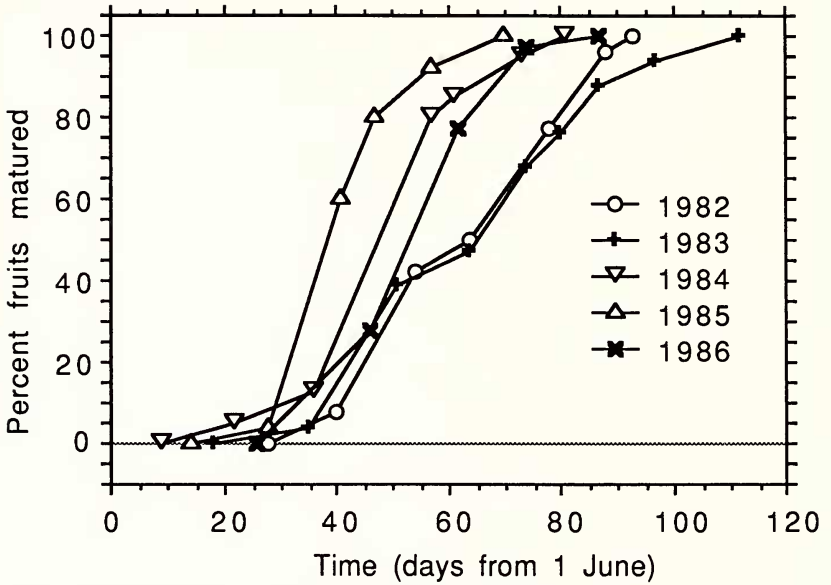
FIG. 1. Timing of fruit maturation of *F. decumbens* during 1982–1986.

Pine Hill *F. decumbens* shrubs into elaiosome and seed portions and, after drying (80°C until constant weight), used four small (1.6–2.6 g) samples of each material to measure total energy contents.

RESULTS

*Ant activity and seed availability.* The timing of ant activity was strongly influenced by temperature. During late winter and spring, ants were active during midday. In late spring and summer the ants switched to foraging in the early morning or at dusk, when temperatures were less extreme. An ant nest entrance usually was abandoned after several months of activity.

Capsule dehiscence spanned a period of time between 41 d (1985) and 77 d (1983). The correlation between period of dehiscence and total capsule production by the monitored branches was inverse (−0.306), indicating that the larger capsule crops tended to mature in shorter periods of time. This correlation was not statistically significant (Fisher's r to z, n = 5, P = 0.655) (Abacus Concepts 1992).

Dehiscence was first noted during late June or early July and was completed by early August or mid-September in each of the five years studied (Fig. 1). Years differed in the rapidity with which capsules matured, and the differences corresponded inversely with mean annual rainfall. Slopes of the curves in Figure 1, visually assessed from Figure 1 and listed by year from high to low have
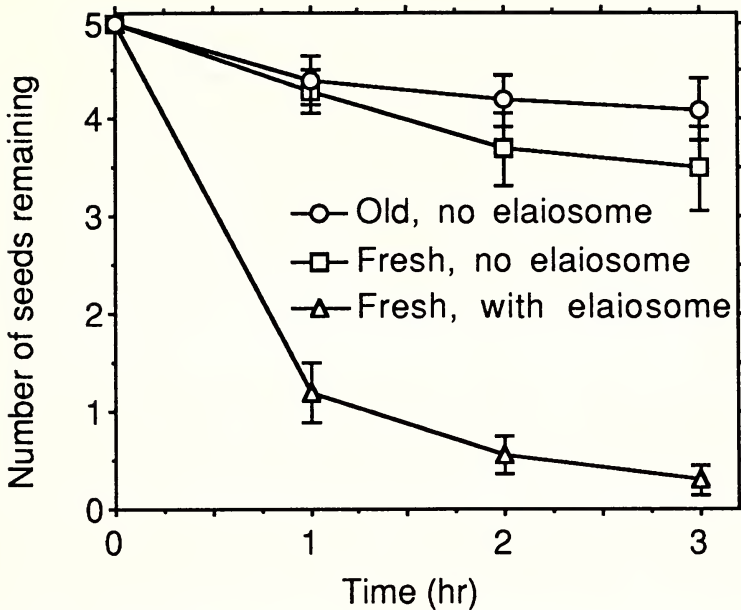
FIG. 2.    Removal of *F. decumbens* seeds from caches by foraging *M. andrei* workers.
Values are means with SE denoted by error bars.

the following order: 1985, 1984, 1986, 1982, and 1983. Precipitation
for these years (as percent of average) and listed from low to high
follows the same order of years: 1985 (71%), 1984 (74%), 1986
(105%), 1982 (165%), and 1983 (202%).

*Harvester ants as seed dispersers.* Harvester ants rapidly removed
fresh elaiosome-bearing seeds, taking almost all intact diaspores af-
ter 3 h (Fig. 2). Seeds lacking elaiosomes were removed very slowly
regardless of whether the seeds were fresh or old. Removal rates
differed significantly between the three seed types at each of the
census times (1, 2 and 3 hr, Kruskal-Wallis test, $P < 0.001$ for each
census time). In all cases, nonparametric Tukey-type multiple com-
parisons (Zar 1984) revealed that the removal rate of seeds lacking
elaiosomes was not significantly affected by seed freshness, whereas
the removal rate of elaiosome-bearing seeds was significantly faster
than that for seeds lacking elaiosomes ($P < 0.001$).

Seeds of *F. decumbens* were frequently found on ant middens,
although the probability of encountering a seed decreased as the
distance from the midden to the nearest *F. decumbens* shrub in-
creased. *Fremontodendron decumbens* seeds were found on 55% of
44 ant middens examined. The majority of middens within 8 m of
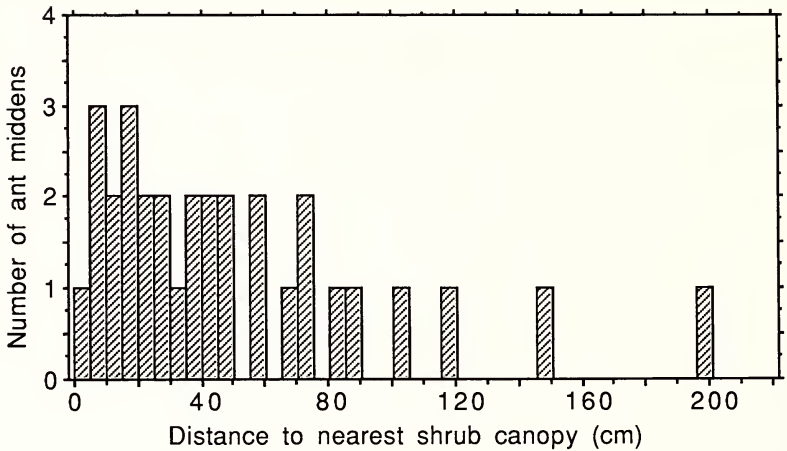a *F. decumbens* shrub contained at least one *F. decumbens* seed.

Fig. 3.    Distances from the entrances of ant nests to the edge of the nearest shrub canopy.

Percentages of middens with *F. decumbens* seeds present were 86% at 0–2 m distant (n = 7), 60% at 2.5–4 m (n = 15), 58% at 4.5–6 m (n = 12), and 60% at 6.5–8 m (n = 5). At distances greater than 8 m, middens with *F. decumbens* seeds became much less frequent (14%, n = 7). The greatest dispersal distance measured was that of a seed found on an ant midden 12 m from the nearest *F. decumbens* shrub.

Ant middens were never found under the canopy of any shrub species. Distances from nest entrances to the edge of the nearest shrub canopy ranged from 0–200 cm, with most (87%) within 1 m (Fig. 3). All of the 39 ant middens examined were at least 35 cm from the edge of the canopy of the nearest *F. decumbens* shrub.

Numbers of seeds found on middens with at least one *F. decumbens* seed ranged widely (from 1–75), although most middens (93%) had less than 10 seeds. There was little correlation between distance from a midden to the nearest *F. decumbens* shrub canopy and the number of seeds counted on that midden. Seed numbers were log-transformed to better meet statistical assumptions underlying correlation analysis (Zar 1984). The correlation between distance and the log of seed number was only −0.16 and was not statistically significant (Fisher's r to z, n = 20, P = 0.767) (Abacus Concepts 1992).

Most seeds recovered from ant middens were relatively close to the nest entrances (Fig. 4). The greatest number of seeds was found 11–15 cm distant, but the curve was distinctly asymmetric, with a few seeds found at relatively great distances. Only 3% were found
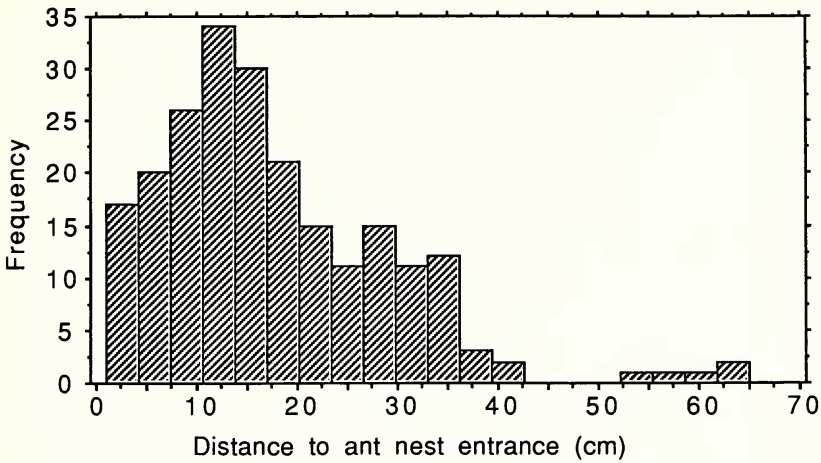
Fɪɢ. 4.    Distances of *F. decumbens* seeds from the entrances of ant nests after seeds are discarded by *M. andrei* workers.

more than 50 cm from the nest entrance and none were found be-yond 65 cm (Fig. 4).

*Fates of seeds taken by ants.* Only 47% of 785 marked diaspores taken by ants were recovered, and for most of these (45% of the total) the seed portion remained intact. The majority of recovered marked seeds, and the unmarked seeds found on the same middens, were ejected by ants after the elaiosome was completely removed (Table 1). Elaiosomes on a small percentage of both marked and unmarked seeds were intact or only partially removed. Some seeds were not recovered intact, but as empty seed coats. Nail polish marks indicated that these seed coats were from seeds supplied to the ants during the experiment. Based on these empty seed coats, at least 5% of the marked seeds were destroyed (Table 1). Almost 11% of unmarked seeds also consisted of seed coats from destroyed seeds (Table 1).

Seeds rapidly disappeared from the five middens monitored for

Tᴀʙʟᴇ 1.    Sᴜᴍᴍᴀʀʏ ᴏꜰ Cᴏɴᴅɪᴛɪᴏɴs ᴏꜰ *F. ᴅᴇᴄᴜᴍʙᴇɴs* Sᴇᴇᴅs Rᴇᴄᴏᴠᴇʀᴇᴅ ꜰʀᴏᴍ *M. ᴀɴᴅʀᴇɪ* ɴᴇsᴛ ᴍɪᴅᴅᴇɴs.

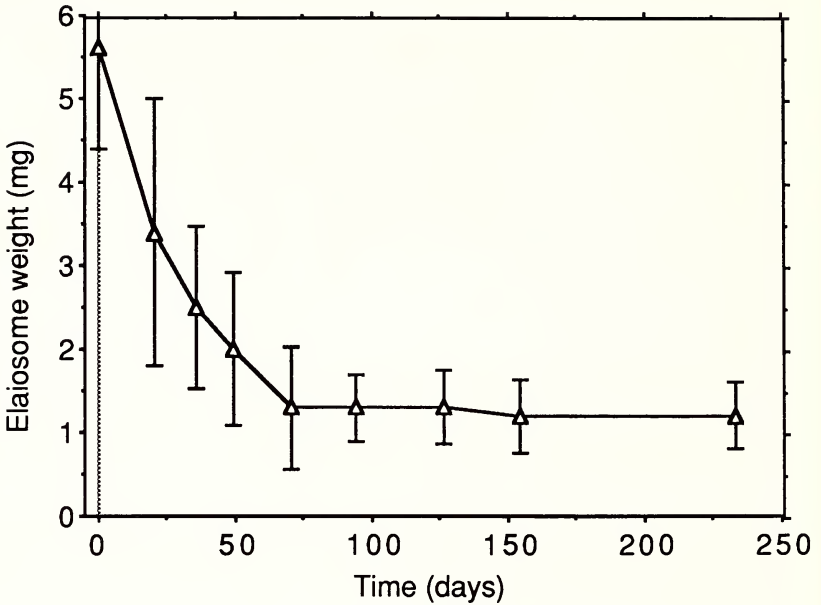| Description | Marked seeds (n = 369) | Unmarked seeds (n = 120) |
|---|---|---|
| Seed intact, elaiosome removed | 92.4% | 84.2% |
| Seed intact, elaiosome damaged | 1.1% | 4.2% |
| Seed intact, elaiosome intact | 1.6% | 0.8% |
| Seed destroyed | 4.9% | 10.8% |

Fig. 5.    Mean elaiosome weights (SD denoted by error bars) graphed against time after placement of seeds in the litter under *F. decumbens* shrubs.

seed removal. After 10 d, 48% remained and after 30 d only 16% were left. At 58 d 8% remained, and they were still present when monitoring ceased at 140 d.

Seed coat thickness under the elaiosome was 3-fold greater than at other places on the seed. Mean thicknesses (in mm, ± SD) were 24.3 ± 3.21, 8.07 ± 0.963, and 7.98 ± 0.839 for the elaiosome end, opposite end, and middle measurements, respectively. Seed coat thickness varied significantly (ANOVA, $P = 0.001$), with significant pairwise comparisons for all but the comparison between the opposite end and middle measurements (Fisher PLSD test, $P < 0.05$).

*Elaiosome longevity.* Elaiosome weight decreased to a constant value within 70 d (Fig. 5). By the end of that period, the orange, waxy portions of the elaiosomes were gone, leaving only hard seed coat-like material at their bases. Elaiosomes declined in weight after only 19 d in the field (Fig. 5). Examination of that sample of elaiosomes showed that some had been chewed by invertebrates which were small enough to penetrate the protective screens. Significant rainfall began October 11, with 2.9 cm falling on that date (NOAA 1983). Litter moisture was relatively high after that time, and I observed elaiosomes with mold on them in the October 23 collection.

TABLE 2.   WEIGHT, CALORIC CONTENT, AND NUTRITIONAL COMPOSITION OF ELAIOSOMES
AND SEEDS OF *F. DECUMBENS*. Standard deviations and sample sizes are provided for
replicated measurements.

| Characteristic measured | Seed | Elaiosome |
|---|---|---|
| Fresh weight (mg) | $33.7 \pm 3.91$ (n = 813) | $3.39 \pm 1.09$ (n = 858) |
| Moisture (%) | $0.96 \pm 0.48$ (n = 3) | 4.3 |
| Crude protein (%) | 11.6 | 21.3 |
| Crude fat (%) | 20.4 | 13.7 |
| Soluble carbohydrate (%) | 40.2 | 45.6 |
| Fiber (%) | 23.6 | 15.4 |
| Ash (%) | 4.15 | 4.00 |
| Total energy (J/mg) | $26.3 \pm 0.569$ (n = 4) | $23.8 \pm 0.133$ (n = 4) |
| Dietary energy/unit (J) | 571 | 55.8 |
| Total energy/unit (J) | 878 | 77.1 |

*Nutritional analysis.* Elaiosomes of *F. decumbens* contained 4-fold more moisture than seeds, but because moisture contents of both were extremely low (Table 2), the dry weight of elaiosomes was 9.7% that of seeds. Elaiosomes contained almost twice as much crude protein and had less fat than seeds, but soluble carbohydrate contents were similar (Table 2). Total energy content of elaiosomes was 2.5 J/mg lower than seeds. Because of the great difference between the two in weight, seeds contained about an order of magnitude more dietary and total energy than elaiosomes (Table 2).

## DISCUSSION

Harvester ants are generally viewed as seed predators (granivores) and hence negatively affect plant populations (Brown et al. 1979; Reichman 1979). Müller 1933 (in Berg 1975) suggested that the presence of harvester ants in the Mediterranean garigue explained the low percentage of myrmecochorous plant species found in that vegetation type. Since then, studies in Australia have shown a relatively large contingent of myrmecochorous plant species in an area where harvester ants are an important component of the ant fauna (Berg 1975). Studies in both Australia and South Africa have demonstrated that myrmecochory is relatively common on infertile soils in both continents (Milewski and Bond 1982). In California chaparral, only two shrub genera have been demonstrated to be ant-dispersed: *Dendromecon* (Berg 1966; Bullock 1974; 1989) and *Fremontodendron* (this study). Seeds of both species bear elaiosomes and dispersal of both involves harvester ants. Despite a relative lack of studies on dispersal mechanisms, ant-mediated dispersal of California chaparral shrub species seems a genuinely scarce phenomenon (Keeley 1991). It should be noted, however, that ants in chaparral move seeds of many species, including shrub species other than

the two noted above. For example, harvester ants have been observed transporting seeds of *Ceanothus* (Horton and Kraebel 1955; Davey 1982; Mills and Kummerow 1989), although they do so to feed upon the seeds themselves. Ant-mediated dispersal of such unspecialized seeds may occur if some seeds escape destruction by the ants. If so, then ant-mediated dispersal may be more important in chaparral than has been thought previously.

Harvester ants may be valuable ant members of a myrmecochorous mutualism with *F. decumbens* for three reasons. First, they are relatively large ants and the seeds of *F. decumbens* are also relatively large (Keeley 1987). This size correspondence allows single workers to pick up and transport single seeds (Beattie et al. 1979). Second, because these large ants may cover large distances from the nest when foraging (Cook 1953), dispersal distances may be great. For example, Gordon (1980) reported that the desert species *Messor* (=*Veromessor*) *pergandei* (Mayr) foraged up to 100 m away from the nest. In a study of dispersal of *Dendromecon,* Bullock (1989) reported that *Pogonomyrmex* harvester ants dispersed seeds "tens of meters". In this study I documented a dispersal distance of at most 12 m, but I suggest that greater dispersal distances probably can occur. In contrast, maximum dispersal distances of elaiosome-bearing seeds dispersed by small ants may be shorter. Examples include 1.5 m for *Viola* seeds (Culver and Beattie 1978) and 3.3 m for seeds of *Trillium* (Ohara and Higashi 1987). Finally, both this study and Bullock (1989) report that harvester ant nests in chaparral are typically located in openings away from the canopies of nearby shrubs. This may result in an increased probability of establishment for ant-dispersed seeds. Seedlings produced in these openings (after germination is stimulated by fire) will likely experience lessened competition from pre-existing shrubs and may have a greater likelihood of surviving to maturity.

Harvester ants also have drawbacks as seed dispersers. As discussed below, their activities as seed predators cause some loss of collected *F. decumbens* seeds. It has even been suggested that the evolution of ballistic dispersal of seeds of *Ceanothus* is an adaptation that results in lower predation of *Ceanothus* seeds by ants (Zammit and Zedler 1988). Harvester ants also leave seeds aggregated on the surface of middens, where they may be subject to increased predation. Bullock (1989) reported some rodent predation and substantial bird predation of *Dendromecon* seeds on middens. In this study, I documented rapid initial disappearance of seeds from middens. Rodent and bird predators likely were responsible.

Many authors (e.g., Berg 1975; Bond and Slingsby 1983) report that the seed portion of diaspores is not harmed when collected and processed by ants to remove the elaiosomes, although careful studies by Hughes and Westoby (1992) indicate this is not always the case.

Even harvester ants have been reported to discard seeds unharmed on their middens (O'Dowd and Hay 1980; Bullock 1989). Keeley (1991) suggested that the elaiosome of ant-dispersed seeds functions as a "bribe" that keeps ants from focussing their predatory activity on the attached seed. In this study, the elaiosome "bribe" was only partly successful. Ants destroyed some seeds taken into their nests, as evidenced by the empty *F. decumbens* seed coats found on their middens. It is possible that these seed coats had been left by another predator that encountered seeds on middens and destroyed them in place. For example, Boyd and Serafini (1992) reported that rodents consumed seeds of *F. decumbens*. However, seeds taken by rodents in that study were not consumed in place, as seed coats were not found in the feeding trays when seeds disappeared from them. This suggests that the seed coats found on the ant middens were ejected from the nests in that condition by the ants and that ants therefore did destroy these seeds.

The percentage of seeds destroyed by the ants can only be estimated. Only 4.9% of marked seeds recovered from ant middens had been destroyed, compared to 10.8% of unmarked seeds. However, these values probably under-represent losses from ant predation, as the fates of 53% of marked seeds were unknown because they were never recovered. Some of these may have remained underground, and some may have been ejected from nests but removed by rodents, but it seems likely that some were destroyed by ants and not represented by the empty seed coats I encountered on the middens. Therefore, in addition to acting as a seed disperser for *F. decumbens, Messor andrei* also acts as a seed predator, consuming at least 5% of the seeds transported.

The increased (3-fold) thickness of the seed coat under the point at which the elaiosome is attached to the seed suggests a defense mechanism that has evolved to limit the predatory component of the ant's activities. Because they consume seeds, harvester ants are generally viewed as having limited value to plants as seed dispersers (van der Pijl 1972). The thickened coat of *F. decumbens* seeds may be an adaptation that protects the seed and allows for successful harvester ant-mediated seed dispersal. This adaptation may not be limited to plants with seeds dispersed by harvester ants. For example, Bresinsky (1963) noted that some plant species from habitats lacking harvester ants have elaiosomes that are separated from the corresponding seed by special thick-walled tissues. It should also be noted that seeds of many plants contain toxins (Carroll and Janzen 1973), so that defense of *F. decumbens* seeds against predation by harvester ants may not be limited to the morphologic one reported here.

The elaiosome of *F. decumbens* has an important function in stimulating ants to disperse seeds. It also has a cost to the plant. Costs

of adaptations can be difficult to determine (e.g., Simms and Raush-
er 1987), in part due to the variety of choices regarding the "cur-
rency" in which those costs are paid. Based on energy values (Table
2), the energetic cost of building elaiosomes reduced *F. decumbens*
seed output by 8%. The energetic investment of *F. decumbens* in
the elaiosome portion of a diaspore is similar to that of other ant-
dispersed species in arid areas. Buckley (1982) summarized Austra-
lian myrmecochores as having elaiosomes that represented 5–10%
of diaspore mass and energy contents. Bullock (1989) reported that
the elaiosome of *Dendromecon* represented 14% of the energetic
value of the entire diaspore, an almost 2-fold greater energetic in-
vestment than that reported here for *Fremontodendron.* It should be
noted that Westoby et al. (1982) suggested that the cost of elaio-
somes for Australian myrmecochores may be more accurately re-
flected by their phosphorus content, because phosphorus was more
limiting than energy in those habitats. Whether energy is the most
appropriate "currency" for measuring cost of dispersal in California
chaparral is not known.

The elaiosome of *F. decumbens* is colored (yellow-orange) rather
than the white color typical of an ant-attractive elaiosome, and hence
is similar to the arils of bird-dispersed species (Davidson and Mor-
ton 1984). Otherwise, the elaiosome of *F. decumbens* has features
that are typical for an ant-dispersed species. Bresinsky (1963) qual-
itatively examined elaiosomes of many ant-dispersed species and
reported that their elaiosomes contained significant amounts of fat,
sugar, and protein. Davidson and Morton (1984) used quantitative
techniques in their examination of the characteristics of arillate Aus-
tralian *Acacia* species. Compared to their results, the elaiosome of
*F. decumbens* is generally low in lipid, high in carbohydrate, and
intermediate in protein content. Thus, it was most similar to the ant-
dispersed *Acacia* species, rather than those dispersed by Australian
birds. It also is very low in moisture (4.3%). This value is lower
than that for any of the 19 species in Davidson and Morton's (1984)
study. The low moisture content of elaiosomes in chaparral areas
has been noted before for *Dendromecon,* and is explained as an
adaptation that allows the elaiosome to persist in the relatively dry
Mediterranean-type climate typical of these areas (Berg 1966).

The low water content of *F. decumbens* elaiosomes may aid in
their longevity, but the elaiosome longevity study showed that elaio-
somes disappeared from seeds within 2 months of their being placed
into the litter layer. There were two reasons for this. First, elaio-
somes were attacked and eaten by small invertebrates. This repre-
sents competition for elaiosomes between harvester ants and these
small invertebrates. Seed dispersal probably does not result from the
feeding activities of these small invertebrates. In a study of *Trillium,*
Ohara and Higashi (1987) showed that ground beetles competed

with ants for elaiosomes. Damage to elaiosomes by the feeding activity of beetles seriously interfered with the ant-plant mutualism, so that 85% of seeds produced were not dispersed away from fruiting plants. Second, elaiosomes rotted when the litter had been moistened by rains. This again represents competition with harvester ants for the elaiosomes, and probably also results in dispersal failure by destroying the ant-attracting component of the diaspore. Because of the activities of these competitors, seeds of *F. decumbens* must encounter a dispersing ant fairly soon after being shed from the capsules. The release of *F. decumbens* seeds over a period of ca. 2 mo may help ensure that at least some seeds encounter dispersing ants prior to elaiosome destruction.

The function of the elaiosome in stimulating ants to disperse seeds of *F. decumbens* is clear, and corresponds with many other studies of elaiosome-bearing seeds (e.g., Marshall et al. 1979; Bond and Breytenbach 1985; Brew et al. 1989; Oostermeijer 1989; Hughes and Westoby 1992). Conversely, it can be concluded that seeds of *Fremontodendron* lacking elaiosomes would not be dispersed by ants. It is interesting to note that Kelman (1991) reported that seeds of a specimen of *F. californicum* lacked elaiosomes. Furthermore, *F. mexicanum* Davidson was reported to have either a small or (more frequently) no elaiosome on its seeds (Kelman 1991). Howard (1950) reported that many chaparral areas lack harvester ants. It would be interesting to know if harvester ants are present at the sites on which these plants grow. In addition, how (or if) *Fremontodendron* seeds lacking elaiosomes are dispersed merits investigation.

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